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Observations on the Acoustic Behavior of Crocodilians

(Figures 1-6)

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Laboratory and field observations were obtained for some acoustic behaviors of *Alligator mississippiensis*, *Caiman crocodilus*, *Crocodylus acutus*, and *Melanosuchus niger*. Tape recordings and sonographs of several call types were obtained.

The young of each species vocalize with a characteristic "bark," which appears to function to announce a threat or food or some other environmental perturbation of significance. No species-specific differences in this call were observed and the spectral characteristics of the call did not vary, except in intensity, with the situation.

Introduction

There is ample documentation of the extent of vocal behavior among the crocodilians; few accounts of any species fail to note its occurrence. Crocodiles are reported to roar and bellow, to hiss, to bark, and to chirp and grunt under a wide variety of ecological and social circumstances. To date, however, no one has attempted to collate these various reports and construct anything approaching an "acoustic ethogram" for any of the species. The vague, contradictory, and often wildly imaginative accounts that comprise much of the literature on crocodilians present a serious hindrance to any such attempt.

This report evaluates some aspects of the ecological and social significance of the acoustic behavior in several species of crocodilians from which laboratory and/or field data were personally obtained. Recordings of the spontaneous vocalizations and of the vocal responses to several experimental situations were obtained from each species in the laboratory and these responses have been verified in natural populations of all species except one (*Melanosuchus niger*). Recordings were usually made with a Sony 400 tape recorder at speeds of three-and-one-quarter or seven-and-one-half inches per second (ips). Exceptions will be noted. Recordings were analysed using a Kay Electric Co., Missilyzer sound spectrograph.

I am most appreciative of the kindness of several individuals in allowing me access to crocodilians in their care, particularly Peter C. H. Pritchard and Jill Goodman. A. Stanley Rand generously assisted me during my field work in Panama and allowed me to report on recordings he obtained. The staff of the Middle America Research Unit, Canal Zone, was of invaluable assistance in every phase of my activities in Panama. Field work in Panama was supported by NIH Grant Ex-00139 to the Center for the Biology of Natural Systems, Washington University. Support for field work in Mexico was from the American Philosophical Society, Penrose Fund, and the New York Zoological Society. The Theodore Roosevelt Memorial Fund of the American Museum of Natural History supported, in part, my studies in Florida. William E. Evans, Naval Undersea Research and Development Center, San Diego, has been of frequent encouragement and assistance in my acoustic studies.

Alligator mississippiensis

The American alligator, both as an adult and when young, is highly vocal. A variety of sounds are produced; the adults characteristically "roar" or "bellow" while the young produce a variety of sounds usually referred to as "barks" or "grunts." The functions of the various calls are open to some question and a diversity of opinions abound.

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The adult "bellow," for example, has variously been considered a mating call, usually ascribed to the male in the breeding season. Neill (1971), however, has pointed out that the call is given by both sexes and at various times of the year. My own observations would support this position, although the call does appear to be involved in courtship and is given by both sexes at this time (Carr, pers. comm.). All references to these calls are anecdotal and no detailed acoustic analysis has been undertaken to determine whether or not differences exist between the bellows of males and females or between the males of different sizes or social status. Such an analysis may reveal differences in the calls which encode such information.

It is, of course, not unusual to find an animal call which transmits information in a social context which varies as a function of the circumstances attending its production and reception. The breeding song of male frogs, for example, encodes vastly different information for another male of the species, an egg-laden female, and a spent female. In squirrel monkeys the relative social status of the recipient individual has been shown to determine the message content of acoustic signals (Winter, Ploog, and Latta, 1966). A similar relationship may well be involved in the social use of the bellow by alligators, both for territoriality and courtship, depending on the hormonal state and social experience of the individuals involved.

The sounds produced by the young also apparently serve diverse functions. They are reported to attract the adult (parent only?) to the defense of the young when they are endangered or alarmed (Neill, 1971). Vocalizations produced by the young before they emerge from the egg are believed to attract the female to the nest and stimulate her to open it to assist in the emergence process (McIlhenny, 1935). These have alternatively been interpreted as a synchronizing stimulus to assure a well coordinated hatch (Lee, 1968). Inasmuch as the female is known to open the nest, on many occasions at least, at the proper time, the first interpretation seems most probable. There is no data to support the contention that hatching in alligator eggs is well coordinated under natural conditions. It is not inconceivable, however, that both functions are involved: the audible vocalizations which begin shortly before hatching serving to attract the female to the nest, and the earlier vibratory stimuli or subaudible vocalization serving to regulate developmental synchrony at earlier periods, much as is the case in many birds (Vince, 1969).

The pre-hatching vocalizations are clearly audible for a distance of 50 feet or more from the nest, even before it has opened, and might well attract predators at a highly vulnerable stage in the species' life history. The adult's presence at the nest and protective response to these vocalizations would certainly be an advantage during this process. It would appear, in fact, that the possibility of attracting predators would constitute a selective disadvantage for this behavioral trait were it not for the presence of the adult at the nest at this time.

In the laboratory, young *Alligator* vocalized readily under several circumstances: during the excitement of group feeding; when startled, frightened, or grasped; and in response to the vocalizations of other crocodilians, either in the flesh or played back from a tape recorder. In the laboratory the initiation of vocalization via tape-recorded playback would result in a series of vocal responses from the captive individuals and a movement toward the loudspeaker. This vocal response and orientation behavior of young alligators could be elicited by a variety of stimuli in addition to the playback of their own calls. The recorded calls of *Caiman crocodilus*, *Melanosuchus niger*, and *Crocodylus acutus* all were equally effective, as were recordings of several lizard vocalizations, the aggressive bark of *Gecko gekko*, and the call of *Ariestelliger praesignis*.

In the field, vocalizations were usually accompanied by short lunges away from the source of disturbance. This would be repeated throughout the group of young with a resulting net group movement away from the disturbance. This vocalization, the characteristic "gnuc," or "bark," of the young, is illustrated in figure 1. No consistent differences detectable on sonograms can be observed between calls given in response to other calls, at feeding stations, or under alarm situations. The one call appears to serve to alert the group members to some environmental characteristic of interest, food, a potential predator, etc., and to maintain some group cohesiveness in the response. The frequent references in the general literature to "distress" and "alarm" calls would appear to reflect the writer's interpretation of the call's significance rather than the alligator's.

The groups of similar aged young (= pods) remain together for at least one season, and perhaps two or three, but nothing is known regarding their composition, whether formed from the young of only one nest or from several; their internal social structure and internal stability, whether pods exchange individuals or not; or what survival function, if any, they subserve. The above discussion, however, would strongly suggest that acoustic signals are significant in maintaining intragroup stability and contact. At night there appears to be an increase in low amplitude spontaneous vocalization by members of the pods. Inadequate data are available to substantiate this point, but one pod monitored for seven hours over three nights and six hours over two days averaged 20 such spontaneous vocalizations (i.e., no environmental stimulus apparent to the inves-

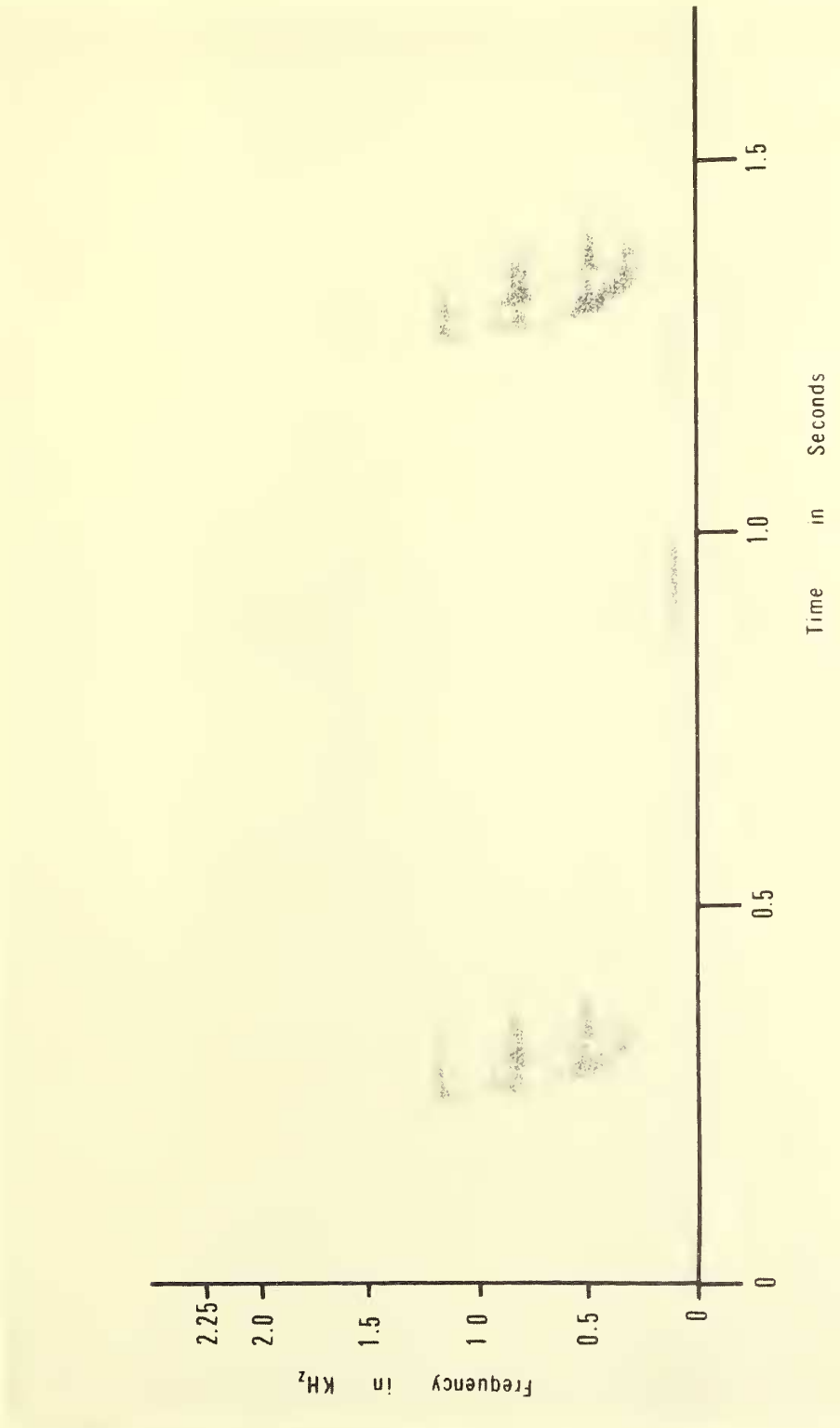

FIGURE 1. Two separate juvenile calls of a hatchling *Alligator mississippiensis*.

tigator) per hour during the night observation periods and only 11 per hour during the daylight periods. This suggests that these low amplitude signals are utilized to a greater degree when visibility is reduced.

Caiman crocodilus

Young *Caiman* are highly vocal in captivity, though perhaps not as much so as young alligators. *Caiman* vocalized readily when startled or restrained and in the midst of group feeding activity, but were less inclined to respond to the vocalizations of other crocodilians. Whereas alligators would respond to a variety of recordings, *Caiman* would only rarely respond to any recordings and then only to recordings of their own species. These observations, while preliminary, may indicate a selective advantage for a species-specific response to acoustic signals in an area where several crocodilian species are in ecological contact (South America) as opposed to an area where only one species exist (central Florida). This, while an appealing hypothesis, is not supported by obvious differences in the calls of the various associated species which might serve for species identification (figure 6).

The behavior associated with the vocalizations was identical to that described for *Alligator*, a vocal response associated with a series of short lunges; this would be picked up by the group with a resulting net group movement.

Under natural conditions in the field in Panama, the response to an intruder was frequently quite different. On being approached there, usually in ponds or river swamp, most individuals would quietly, or after one vocalization, submerge several inches, back up a few inches, and turn to the side, much as described for *Crocodylus novaeguineae* (Neill, 1971). When surprised on land, however, or in very shallow water, escape lunges associated with vocalizations were normally observed. The method of escape utilized appeared to correlate with the depth of water in which the individual was located and, perhaps, with the suddenness of the appearance of the investigator-predator.

Inasmuch as auditory determinations are available for this species, it may be profitable to compare the known auditory sensitivity as determined by electrophysiological methods with the frequency parameters of their call. Manley (1970), studying single units in the cochlear nucleus; Konishi and Campbell (unpubl. data), using the N_1 response recorded at the round window; and Wever (1971), using the microphonics recorded at the round window, determined the frequency zone of maximum sensitivity to lie approximately between 0.2 and 2.0 KHz. This is quite in line with the frequency parameters of the call as illustrated in figure 2. Here the fundamental begins at about 0.7 KHz and sweeps downward to about 0.2 KHz in one-ninth of a second. Several harmonics are present, the first beginning at 1.3 KHz and sweeping downward to 0.3 KHz, and the second beginning at 1.7 KHz and sweeping down to 0.6 KHz.

Crocodylus acutus

Judging from the literature and the behavior of captive young, the American crocodile is much less vocal than either of the preceding species. The young do vocalize before and during the hatching process, however, and recordings of this behavior were obtained by Dr. A.S. Rand of the Smithsonian Tropical Research Institute in the Canal Zone. Vocalization began prior to the actual emergence from the eggs and continued throughout the process. Figure 3 illustrates one of the calls from Rand's recording. The fundamental begins at about 0.6 KHz and downshifts to about 0.3 KHz in one-fifth of a second. Several harmonics are strongly indicated. To the observer the call sounds highly similar to the distress call of very young *Alligator mississippiensis* and *Caiman crocodilus* and to the calls produced by hatching *Alligator*.

Young American crocodiles also utilize a "contact" and/or "distress" call under much the same laboratory circumstances as reported above for *Alligator mississippiensis* and *Caiman crocodilus*.

Crocodylus acutus frequently utters a "snarl" when attacking non-prey objects. This has been observed on several occasions with different individuals, all under three feet in total length. This call is usually given with mouth agape, facing the object, and immediately precedes, or is concurrent with, an attacking lunge. Figure 4 illustrates an example of this call given by a 30-inch specimen from Jamaica when attacking a large turtle which had been placed in its home tank. The call begins at a frequency of 0.3 KHz in one-fourth second, then changes to 1.5 KHz for one-fourth second before abruptly dropping off. Similar "snarls" have been reported in aggressive situations for other crocodilian species, *C. niloticus* (Cott, 1960) and *Melanosuchus niger* (Neill, 1971), for example.

Interestingly, if the initial aggressive response does not result in an alteration of the "threat" situation, the crocodile will alter its behavior to attempted escape or avoidance from the threatening object and begin to vocalize with the juvenile call. Figure 5 illustrates a juvenile call, or "grunt," of the above mentioned Jamaican individual after its initial attacks on the large turtle were unsuccessful. These calls were uttered as the crocodile attempted to climb out of its pen or sat submerged and tail-to the turtle. This call is very similar to the so-called distress calls recorded from the other species, beginning at 0.5 KHz and downshifting to approximately 0.2 KHz

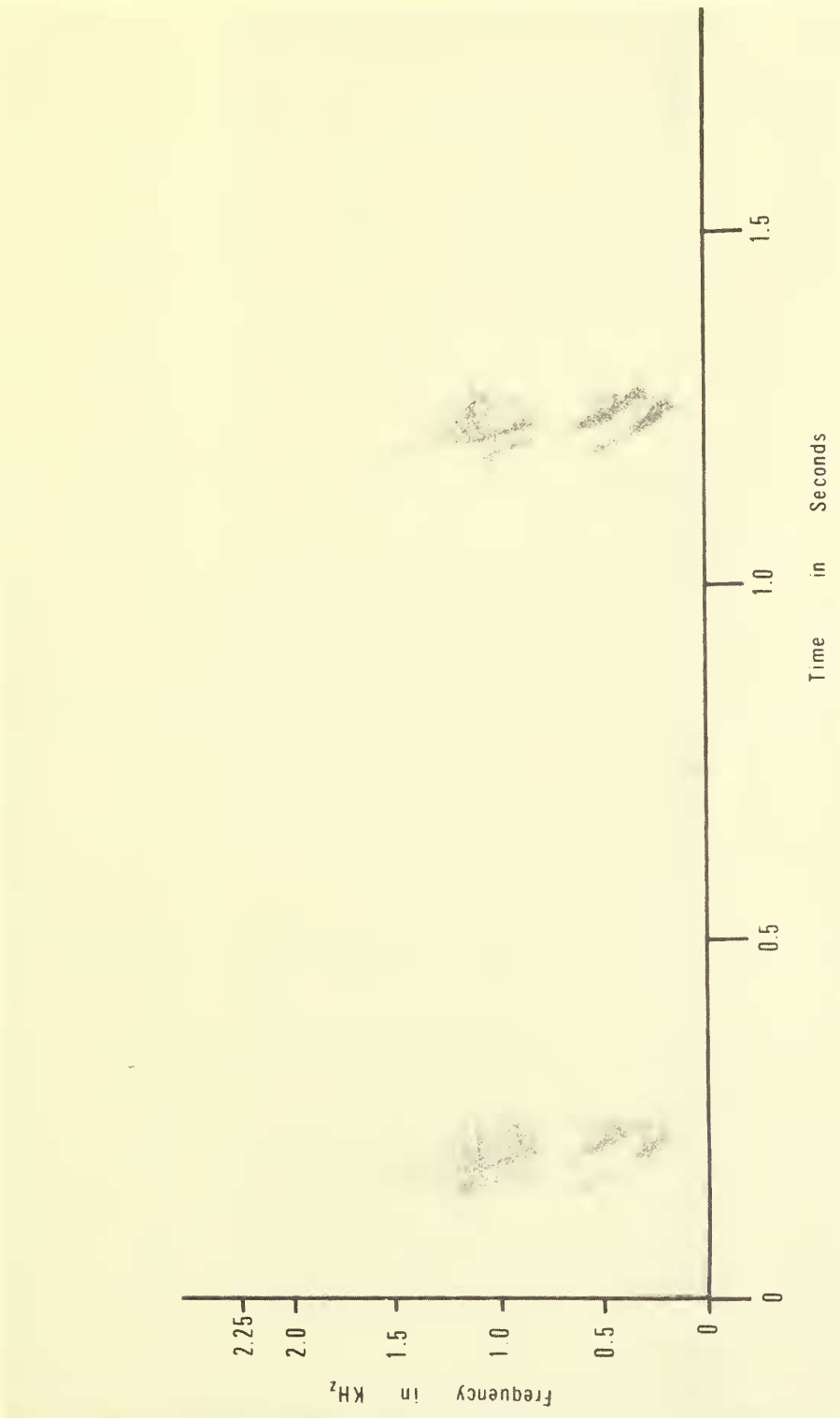

FIGURE 2. Two separate juvenile calls of a 12-inch *Caiman crocodilus*.

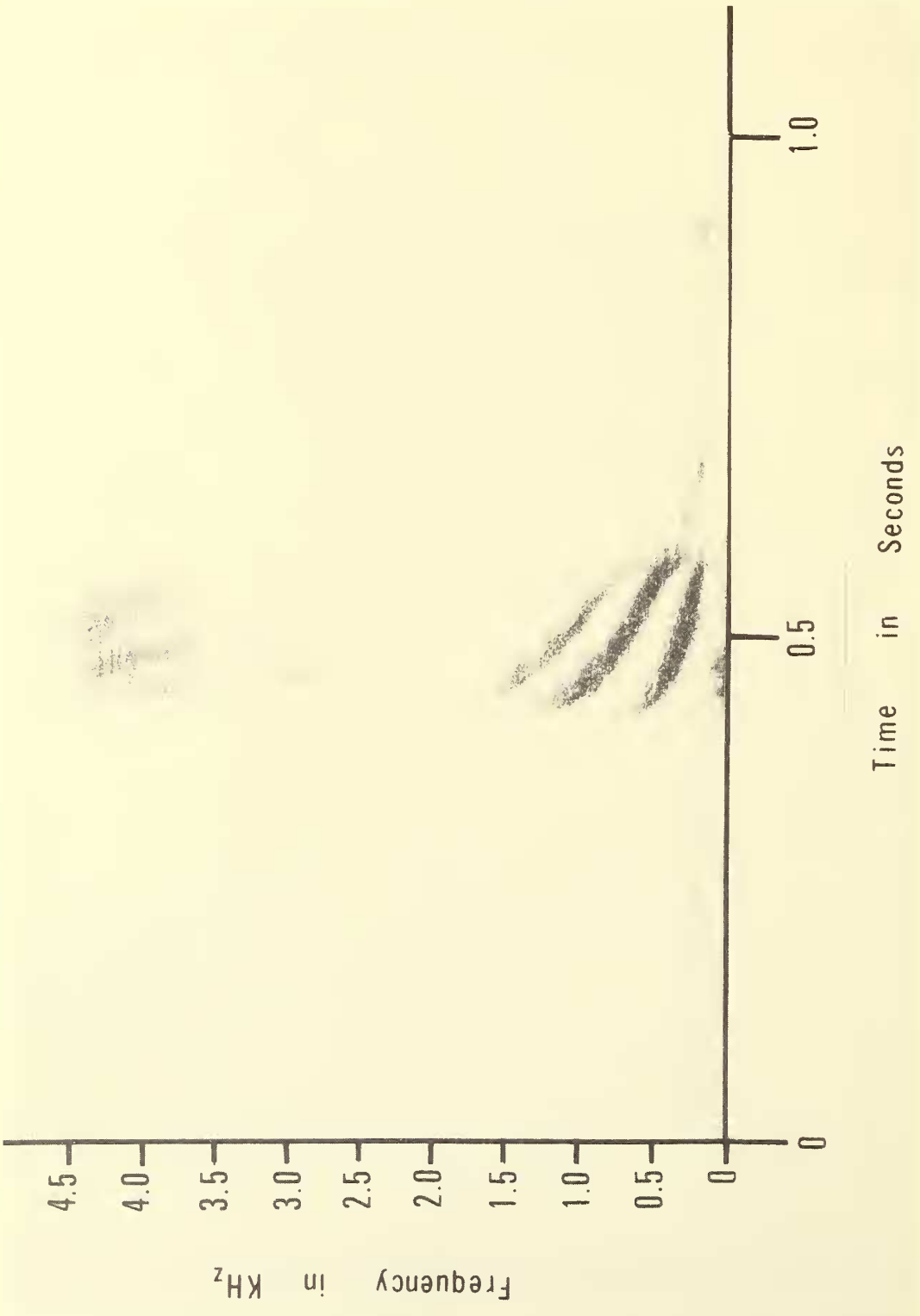

FIGURE 3. Hatching call of *Crocodylus acutus* recorded in Panama by A.S. Rand. Individual was partially emerged from the egg.

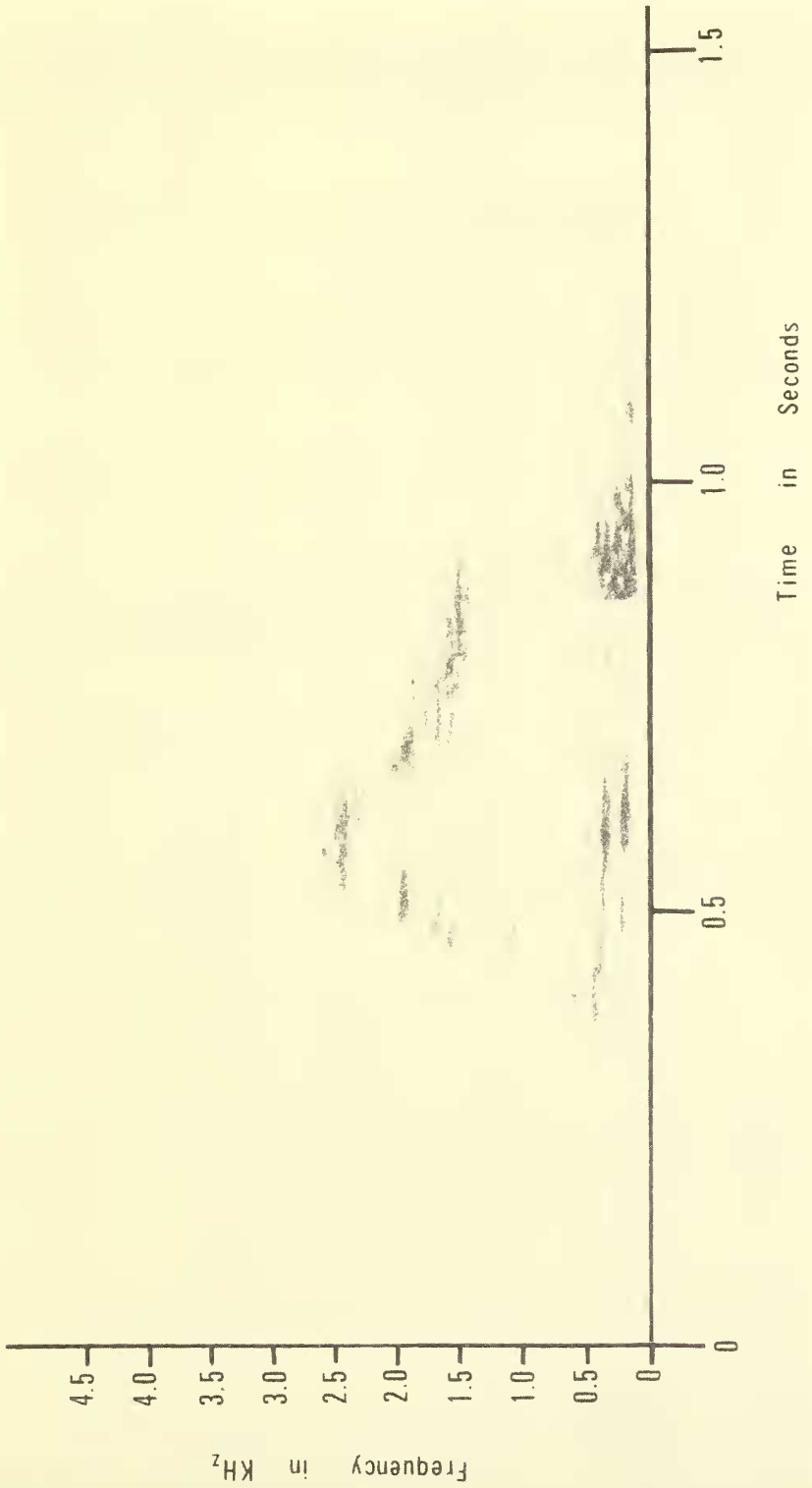

FIGURE 4. Aggressive growl or snarl of 30-inch *Crocodylus acutus*.

FIGURE 5. Juvenile call of 30-inch *Crocodylus acutus* (same recording session as figure 4).

FIGURE 6. Response of an 18-inch *Melanosuchus niger* (second call) to a playback of the juvenile call of a 12-inch *Caiman crocodilus* (first call).

over one-third of a second. This full sequence of behaviors was observed on two occasions with this Jamaican specimen and has since been observed in several other individuals.

Melanosuchus niger

One specimen of *Melanosuchus* was available for study. It was an 18-inch juvenile and had been in captivity for 11 months in the company of other crocodilians prior to its use.

Overall, this individual was much less inclined to vocalize than the specimens of *Alligator mississippiensis* and *Caiman crocodilus* studied. Numerous attempts to obtain recordings were unsuccessful. The specimen would grunt or "bark" on occasion when disturbed, but recordings were not obtained. The specimen showed a positive orientation to playbacks of the calls of *Alligator* and *Caiman crocodilus*, orienting toward the speaker and moving to the close end of the tank, but on only one occasion did it vocalize in response to any recordings. The vocal response to a call of *Caiman crocodilus* is illustrated in figure 6. The first signal is that of the *Caiman*, the second that of the *Melanosuchus*. The call is very similar to that of the *Caiman* but extends to lower frequencies, to 0.2 KHz as opposed to 0.3 KHz. This reflects the larger size of the *Melanosuchus* rather than any species-specific difference in the calls.

As crocodilians grow, their calls, at least the juvenile calls, deepen and include an increased range in the lower frequencies. The calls of 20-inch *Caiman crocodilus* also extend down to 0.2 KHz as does the juvenile call of *Crocodylus acutus* illustrated in figure 5, from a 30-inch specimen. This relationship between body size and pitch has previously been described in other animal groups (Collias, 1960).

Discussion

Crocodilians vocalize under a variety of circumstances, both in the field and in the laboratory. While species-specific variations in vocal tendencies are suggested, the data currently are too anecdotal and incomplete to allow any conclusions on this point. Several types of calls are well established: the bellowing of adults, of unverified function; and a variety of calls produced by juveniles. There appears to be no obvious distinction in structure between the juvenile calls of the various species examined, and the behavioral and environmental correlates of the vocalizations are similar in all species for which data are available.

The most often reported, and most easily evoked, vocalization of the young crocodilian is the "distress" call, a segmented call with an initial down sweep in frequency followed by a short plateau. This resembles the segmented "ground predator" or down sweeping "distress" calls as described by Collias (1960), and appears to function to alert nearby individuals and perhaps to coordinate the group escape response, as well as attracting adults to the area.

The vocalizations produced by hatching individuals of *Crocodylus acutus* resemble the down sweeping distress call of Collias (1960) and function to attract the female parent to the hatching site. Species-specific differences in this behavior may be present, for example Alvarez del Toro (1969) reports both parents participating in the emergence process in *Caiman crocodilus* while only the female is implicated in *Crocodylus niloticus* (Cott, 1960) and the situation in *Alligator mississippiensis* is open to debate (Neill, 1971), or variable. More careful observations on this point are needed.

The other vocalizations reported here, the aggressive "snarl" of *Crocodylus acutus*, and the call given in the presence of food by all species examined, which does not appear to differ from the "contact" or "distress" call, are mentioned throughout the literature for a number of other species. In addition to those mentioned here, a number of other vocalizations have been reported for crocodilians ranging from "coughs" to hisses. At the present time it is difficult to assess the social or ecological function of most reports of crocodilian vocalizations despite the frequency with which these reports occur. The evidence does indicate that the crocodilians are a highly vocal group which utilize acoustic signals in a wide spectrum of behavioral/ecological contexts, and future studies in this area should prove highly rewarding.

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